



## Rapid acceleration in Odonata flight: highly inclined and in-phase wing beating

Georg Rüppell<sup>a\*</sup> and Dagmar Hilfert-Rüppell<sup>b</sup>

<sup>a</sup>Independent scholar; <sup>b</sup>Institute of Science Education, Technical University, Braunschweig, Germany

Acceleration manoeuvres in free flight in nature of five damselfly (Zygoptera) and four dragonfly (Anisoptera) species were analysed by means of slow motion filming. Changes in stroke frequencies, stroke angles, stroke directions, angles of inclination of the wings, and the phase-relationship of fore- and hindwings were recorded during acceleration. Damselflies and dragonflies showed similar actions. In rapid acceleration, a shifting of the relationship of the two wing pairs to in-phase stroking and the use of highly inclined wings in the stroke direction opposite to the flight direction can be seen. Slow backward flight was done by phase-shifted stroking, fast backward flight by in-phase stroking. The downstrokes in slow and fast backward flight were quicker than the upstrokes. When fleeing from frogs, dragonflies show extreme flight action: all stroke phases were in-phase and the stroke phases directed toward the frog were very fast and highly inclined. Distances covered per stroke, non-dimensional flight velocities and acceleration are compared and discussed.

**Keywords:** insect flight; kinematics; acceleration; inclination angles; phase-relationship; Anisoptera; Zygoptera; escape flight; frog predation; take-off; dragonfly

### Introduction

Odonata are large insects; they dominate the air. While other insects have evolved protective adaptations – butterflies with erratic flight, beetles with hard covers, Hymenoptera with poison stings, Diptera with fast flight, together with the very small bodies of many species in some groups, e.g. Hymenoptera and Diptera – Odonata feed on all of them.

In relation to their size, dragonflies and damselflies are amongst the best flyers of all animals. They can avoid predatory birds in flight, hover, fly backward or upward within tenths of seconds. The question arises: how can they be so agile?

Slow-motion studies are necessary to understand the dragonfly success story, which has lasted for more than 300 million years (Rehn, 2003). Odonata flight was not really understood until fairly recently: kinematic and functional studies (Ennos, 1988; Rüppell, 1989; Wakeling & Ellington, 1997a, 1997b, 1997c; Weis-Fogh, 1973; Wootton, 1992) shed some light. The phase-relationship of fore- and hindwings can change (Rüppell, 1989). Odonata are the only insects that are able to move all four wings separately. This enhances their flight ability –but increases the difficulties of analysis as well. This is why dragonfly flight in nature is very rarely investigated. Only Rüppell (1985, 1989) delivered findings on the kinematics of Odonata flight; while Günther, Hilfert-Rüppell, and Rüppell (2014), Günther (2015), Hilfert-Rüppell and Rüppell (2013) and Hilfert-Rüppell have reported variations of flight in a behavioural context. To explain the

\*Corresponding author. Email: [g.rueppell@freenet.de](mailto:g.rueppell@freenet.de)

mastery of Odonata flight a number of sophisticated flow visualisations and experiments have been published (Ellington 1984a, 1984b; Ellington, van den Berg, Willmott, & Thomas, 1996; Lu & Shen, 2008; Maxworthy, 1979; Phillips, Knowles, & Bomphrey, 2015; Saharon & Luttges, 1989; Wang & Russel, 2007). Explanations have been offered for the role of phase-relationships of forewings and hindwings (Bomphrey, Nakata, Henningsson, & Lin, 2016; Lehmann, 2017; Usherwood & Lehmann, 2008) or of wing angles of incidence (Thomas, Taylor, Srygley, Nudds, & Bomphrey, 2004) in flight manoeuvres. But to determine the whole range of flight capability of Odonata, analyses of spontaneous natural flight – and this in extreme situations – are necessary. This paper adds some new results to the developing picture.

The flight of dragonflies is fast, often erratic and unpredictable. So the recording of flight manoeuvres in the field is possible in most cases only with a lightweight movable camera – but then only in 2D projections, which limits the usefulness of the data. But simply knowing how Odonata adjust their wings and body when fleeing or flying for reproductive success could help to understand these successful insects better. This paper focuses on extreme acceleration in forward and backward flight. A further question is: given that the two suborders Anisoptera and Zygoptera differ widely in shape and body size, are their flight actions similar?

## Material and methods

With practice, the choice of good sites and of suitable dragonfly species, and endless patience, it was possible to get sufficient usable flight films for a precise analysis. This material is only appropriate for some measurements, such as temporal patterns like stroke frequencies or phase-relationships between the wings or flight speeds or wing speeds. Filming is most favourable when the dragonflies are flying or moving the wings at right angles to the camera axis. In all other cases in which three-dimensional movements are to be analysed, only approximate results can be obtained.

Digital slow motion cameras (Casio EX F1, Yamagata, Japan, Sony RX 10 II and III, Shenzhen, China) were used. The Casio camera was able to film with sufficient resolution at 300 and 600 f s<sup>-1</sup> for minutes, while the Sony camera operates with better resolution at 250, 500 and 1000 frames for 2 or 4 s. The maximal focal length of the Casio camera was 460 mm, of the Sony RX 10 III 600 mm. The exposure time is adjustable in this model. Thanks to the better resolution of the Sony camera it is possible to use “frame grabs” of the image.

Our main sites were at the river Oker north of Braunschweig, Germany (52.27 N, 10.52 E) and at some ponds near Braunschweig. A very good site is the garden pond situated in front of our study.

The Odonata were filmed at their reproduction sites during warm periods of sunny days from May to September. To avoid disturbing them, the filming author sat virtually motionless at a distance of 1–5 m (in some cases up to 10 m) from the animal. The focus plane was then fixed at the lens. When relevant flight took place in the selected zone, the shutter was released. The prerecord mode of the camera then guaranteed capture of the action.

We moved the camera parallel to the flying dragonflies, following them to and fro and back and forth very quickly by targeting the insects directly, viewing through the viewfinder or on the camera screen only briefly. Films were analysed frame by frame using Quick time<sup>(TM)</sup> (version 7.7.9, Apple, Cupertino, USA). Time data are easy to obtain: if filming at 300 f s<sup>-1</sup>, the separation from one frame to the next is 1/300 s. To obtain the distances covered, a simple method which works only when the insect is large and sharp enough on the film and is flying at right angles to the camera axis was used. If the camera was not moved during filming, one can mark the head of the dragonfly on the screen or piece of paper. Then one advances the film frame by frame until

the tip of the abdomen reaches the marked point. This body length distance can be determined, ideally after having caught this particular specimen, or by taking data from literature (Dijkstra, 2006). With this distance and the elapsed time (= number of frames) one gets the speed of the dragonfly by calculation. A more precise method is to mark the displacement of the body or the wing tip and to correct this distance by the scale, which is determined by the relation of the



Figure 1. Wing twisting of a hovering *Aeshna cyanea* male. These distortions result in decreasing angles of incidence from the base to the tip of the wings. The different view directions shorten the wings and vary the wing angles in such a two-dimensional picture.

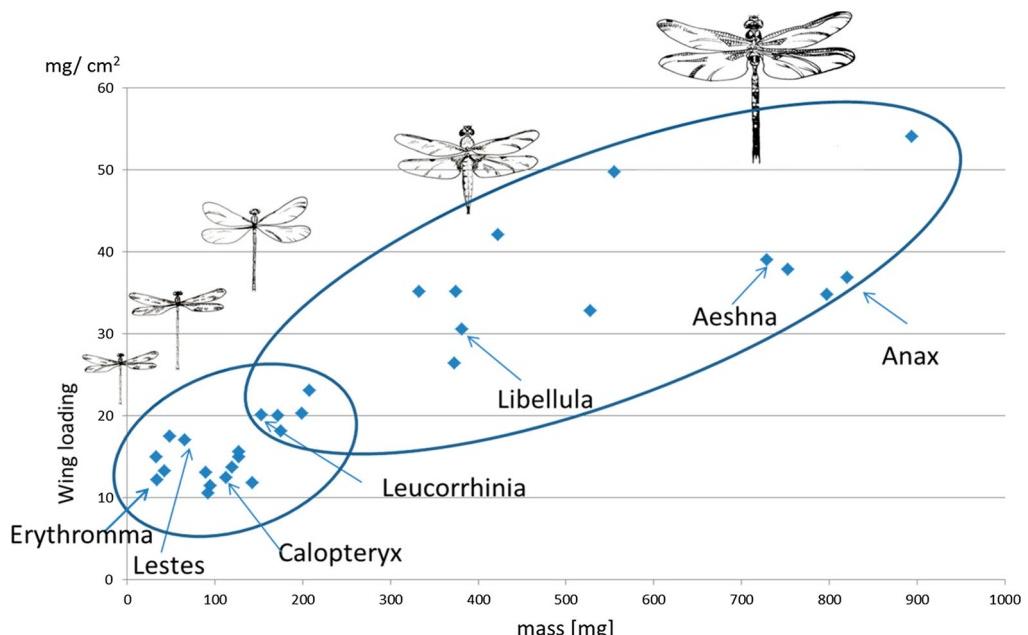


Figure 2. Wing loading over mass of Odonata males. The named genera (the arrows mark the area of data, depending on sex and nutritional status) are males of *Erythromma viridulum*, *Lestes viridis*, *Calopteryx splendens*, *C. virgo*, *Leucorrhinia pectoralis*, *Libellula quadrimaculata*, *Aeshna cyanea* and *Anax parthenope* (of similar size as *A. imperator*). Females are mostly heavier and have a higher wing loading (see Table 1). Varied after Grabow and Rüppell (1995).

Table 1. Morphometric data of filmed species. Body mass and wing-loading from Grabow and Rüppell (1995). The first value is for females (f), the second for males (m). In *Anax imperator* only values for similar sized *A. parthenope* (Ap) were inserted, in *Leucorrhinia pectoralis* those of *L. rubicunda* (Lr); body length and hindwing length (hw length) from Dijkstra (2006; data as a range not differentiated between the sexes).

Species	Body mass (mg)	Body length (mm)	hw length (mm)	Wing loading ( $\text{mg cm}^{-2}$ )
<i>Coenagrion puella</i>		33–35	15–24	
<i>Erythromma viridulum</i> m		26–32	16–20	
<i>Lestes viridis</i> m	66	39–48	23–28	17.1
<i>Calopteryx splendens</i> f, m	120, 156	45–48	27–36	15.9, 13.7
<i>C. virgo</i> m	143	45–49	24–36	11.8
<i>Aeshna cyanea</i> f, m	729, 1098	67–76	43–53	57.2, 39
<i>Anax imperator</i> f, m	779, 821 Ap	66–84	45–52	34.2, 36.9 Ap
<i>Libellula quadrimaculata</i> f	350	40–48	32–40	28.1
<i>Leucorrhinia pectoralis</i> f, m	212, 208 Lr	32–39	30–33	23.7, 23.1 Lr

filmed dragonfly's overall length and a real measure taken from our own measurements or from literature (Dijkstra, 2006). Flight and stroke directions could be determined sufficiently precisely in some cases only.

The stroke angles and the angles of inclination of the wings (= wing angles between wing chord and stroke direction) were difficult to measure. In some cases it was possible to specify these angles by constructing the spatial situation with dragonfly wings, holding them in a similar position to the filmed image. Nevertheless this gave values with up to 20% error rates. When the wing was twisted (Figure 1), only rough estimations could be obtained, because one cannot be certain of the exact position of the relevant cross section of the wing. Angles appear larger when not filmed at right angles, which is difficult to correct precisely.

The non-dimensional flight velocity was calculated (after Ellington, 1984a, 1984b) as the ratio of the distance covered in each wing beat to the wing length.

The filmed Odonata (Figure 2, Table 1) were all undisturbed and flying in their natural surroundings. It was neither possible nor useful to catch them when filming. Their behaviour then would have finished.

## Results

### 1. Acceleration forward

Acceleration takes place at every flight of any dragonfly or damselfly. But to record sharp acceleration one needs to film over a wider area. Unfortunately, details of the wing movements cannot then be detected. From forward flight ( $4.2 \text{ m s}^{-1}$ ), a male *Anax imperator* accelerated to very

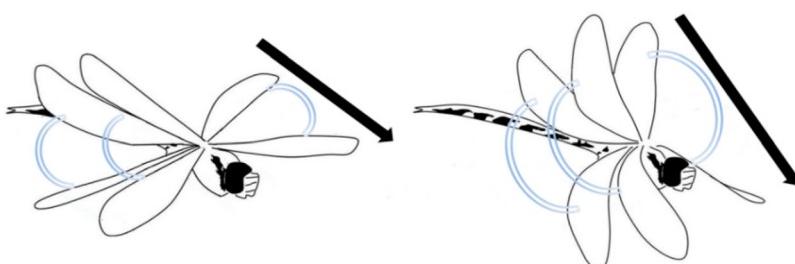


Figure 3. A male of *Aeshna cyanea* increased the stroke angles to accelerate forward and inclined the stroke direction forward down. The stroke angles were: hovering (left) around 50° and accelerating forward (right) between 80° and 110°.

Table 2. Flight mode of Odonata species, flight speed at analysed manoeuvre and acceleration.

Species	Flight mode	Max speed( $\text{m}\cdot\text{s}^{-1}$ )	Acceleration ( $\text{m}\cdot\text{s}^{-2}$ )
<i>Coenagrion puella</i>	Start forward	0.44	1.95
<i>Erythromma viridulum</i> m	Fast backward	1.16	23.2
<i>Calopteryx splendens</i> m	One stroke backward	0.84	9.2
<i>C. virgo</i> m	Backward	0.6	9.7
<i>Aeshna cyanea</i> f, m	Backward	0.59	3.2
<i>Anax imperator</i> f	Fleeing forward	0.57	10.6
<i>Anax imperator</i> m	Forward	7.1	15
<i>Leucorrhinia pectoralis</i> f	Fleeing backward	1.6	40

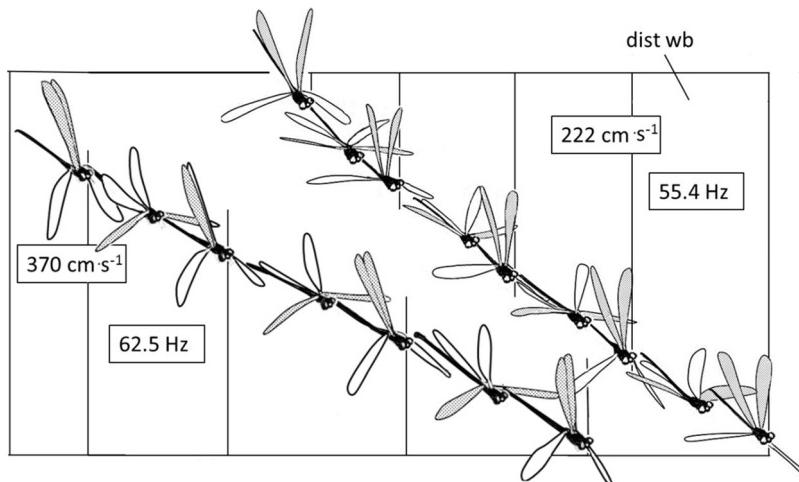


Figure 4. Slow and fast flight of *Erythromma viridulum* males. The right male flew first, the left male pursued the other for attack. Grey wings = forewings, white wings = hindwings. The wings of the left male clapped at the ends of upstrokes together. Dist wb = distance covered by the stroke in question. From a film at  $600 \text{ f s}^{-1}$ .

fast flight ( $7.2 \text{ m s}^{-1}$ ) within 0.2 s, which is an acceleration of  $15 \text{ m s}^{-2}$  (Table 2). Only close-up filming of accelerations occurring over a small range allowed a detailed analysis. In the next sub-sections are some examples of such analyses.

### 1.1. Changing stroke angles, stroke direction and stroke frequency

Increasing stroke angle (= stroke amplitude), stroke frequency and inclining stroke direction forward and down were frequent means of accelerating forward (Figures 3, 4).

In some cases the beat frequency in *A. cyanea* was not increased: 41 Hz in hovering on the spot and 40 Hz accelerating forward ( $N=11$ ). In other cases, e.g. in *Libellula quadrimaculata*, the beat frequency at acceleration increased significantly: hovering on the spot = mean 38.8 Hz, SD 5.5; accelerating forward = 46 Hz, SD 5.8 ( $p = 0.002$ , Mann–Whitney U,  $N=12$ ).

In a pursuing flight of two *Erythromma viridulum* males, flight parameters differed considerably: the faster pursuer had a higher beat frequency and used wider stroke angles. He covered about  $100^\circ$  with the forewings and about  $85^\circ$  with the hindwings, the slower flyer about  $57^\circ$  with forewings and about  $54^\circ$  with hindwings. Furthermore, the pursuing male clapped the wings together at the end of each upstroke. The flight speed and the distance covered by one wing beat differed significantly:  $0.37 \text{ m s}^{-1}$  to  $0.22 \text{ m s}^{-1}$  and  $0.032 \text{ m}$  ( $N=4$  wing beats) to  $0.046 \text{ m}$  ( $N=3$  wing beat (wb), Figure 4, Table 1).

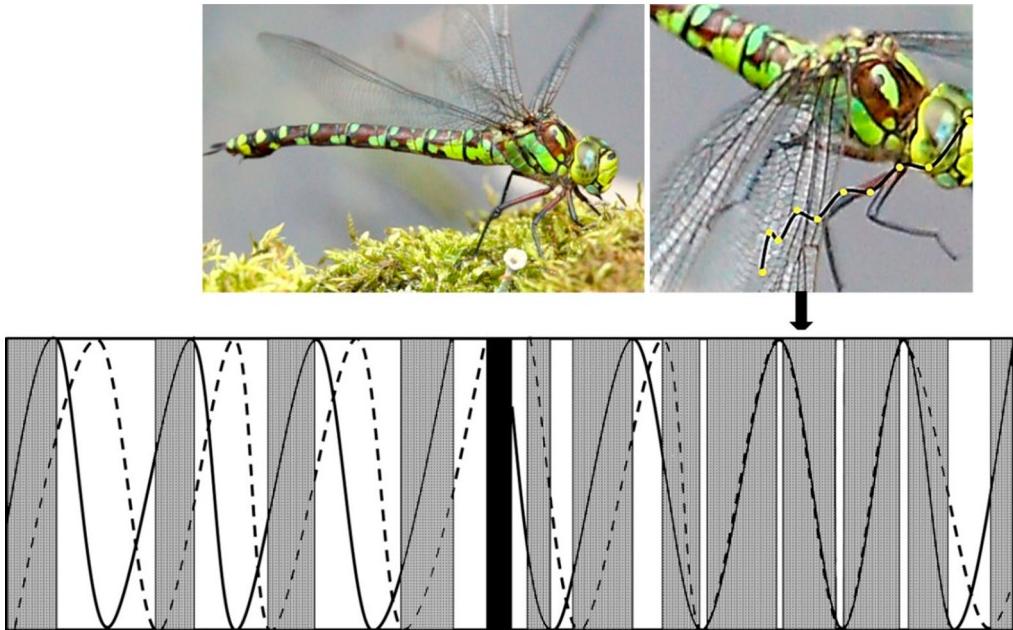


Figure 5. Phase-relationship of hindwings (solid lines) and forewings (broken lines) at forward flight of a male (bottom left to the black area) and starting flight of a female *Aeshna cyanea* (right, bottom and both pictures above). The lines symbolise the downstrokes (down-going lines) and upstrokes (up-going lines). In forward flight 38.1% of the stroking was done in-phase, while at take-off this was about 80%. The curve in the right photo shows the distance gained by successive downstrokes (1st, 3rd, 5th, 7th and 9th sections longer, more vertical lines) and by upstrokes (shorter, more horizontal lines). Arrow: moment of take-off. Filmed at 1000 f s<sup>-1</sup>.

### 1.2. Changing phase-relationship

When accelerating sharply, the phase-relationship of fore- and hindwings changes toward more in-phase beating. In normal flight situations this occurs only when the flight direction is more upward or backward (Figure 5).

### 1.3. Changing wing angle between down- and upstroke and phase-relationship

During sharp acceleration, for example at rapid take-offs, there was a clear difference between the inclination angles of up- and downstrokes. This was the case in a teneral *Coenagrion puella* fleeing the fast approaching camera of the author (Figure 6).

These angles differed by around 70–80° between down- and upstroke. The wings at down-stroke were seen filmed from above in nearly their full shape, while during upstrokes they were represented only by a thin line. The relation in this fast forward acceleration of *Coenagrion puella* was 38.2% upstroking in-phase at high-inclined wings, 27.4% downstroking in-phase at low-inclined wings and 37.1% not in-phase (in the three strokes after one stroke at take-off at 28.6, 25 and 20 Hz, Figure 6), while in another teneral *C. puella* flying on the spot the in-phase part of upward stroking was only 13.8% (4 wb: 26.4 Hz) and the not-in-phase relation was 71.3%.

## 2. Acceleration backward

All Odonata species showed backward flight. In all cases there was a change of stroke direction to a more raised course, often horizontal or even more erected in front (Figures 7, 8). There are

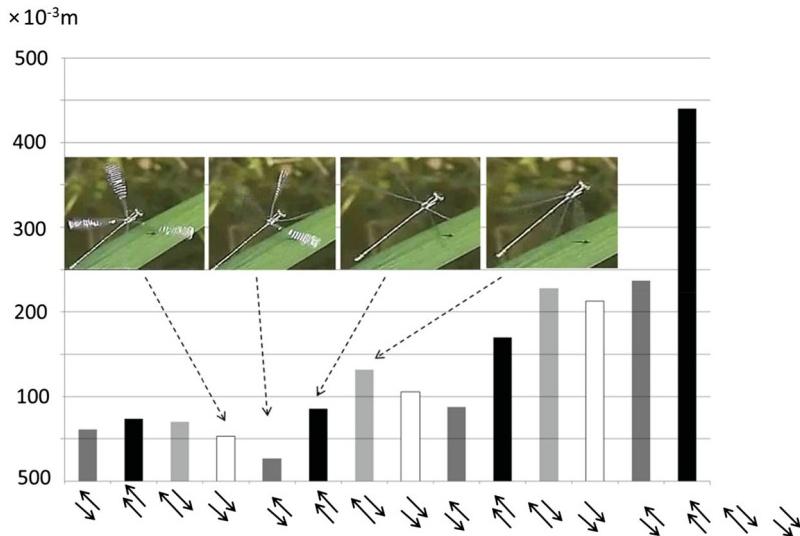


Figure 6. Flight speed (ordinate) in a quick forward start of a teneral *Coenagrion puella* male with four strokes. Photos from left to right: (1) forewings and hindwings down stroking = white bars and both arrows downward; (2) forewings beginning upstroke, hindwings down stroking = dark grey bars and arrow above up, arrow below down; (3) both wing pairs up stroking = black bars and both arrows up; (4) forewings beginning downstroke hindwings ending upstroke = light grey bars and arrows above down and arrows below up. Camera view from above. The wings were beaten at upstrokes at high wing angles (3rd photo: damselflies with thin wings) and at downstrokes (1st photo: broad wings) slightly inclined. From a film at  $600 \text{ f s}^{-1}$ .



Figure 7. Backward flight of *Aeshna cyanea* female. Beginning at first row above from left (phase 1) to right. The body axis is erect. The wings are beaten phase-shifted and at small inclination angles backward (left hindwing 8th and 9th phase; left forewing 1st, 2nd, 3rd phase) and at large angles downward (left hindwing 1st, 2nd, and 3rd phase; left forewing 6th, 7th and 8th phase).

differences in doing it fast or slowly. Most strikingly, the inclination angles of the wings were varied, and so was their stroke velocity and the phase-relationship of fore- and hindwings.

### 2.1. Slow backward flight by phase-shifted stroking

*Aeshna cyanea* flew slowly ( $0.59 \text{ m s}^{-1}$ ) backward with seven recorded phase-shifted strokes. The in-phase proportion of the whole stroke duration was 46.3%. The stroke frequency was 44.4 Hz ( $N=5$ ), slightly higher than in accelerating flight (40.7 Hz, SD 2.16,  $N=10$ ) or when hovering on the spot (41.7 Hz SD 2.3,  $N=10$ ). The ratio of down- to upstroke duration was 1:1.4.

The hindwings led the motion by 25.9% ( $= 93^\circ$ ), about  $\frac{1}{4}$  of a period. The maximal wing-tip velocity at the third downstroke (high inclined wings) was  $4.5 \text{ m s}^{-1}$  (measured in the middle of stroke) and at the fourth upstroke (slightly inclined wings)  $6.2 \text{ m s}^{-1}$  (measured) at the upstroke. The acceleration was steady (Figure 8). The stroke angle was about  $80^\circ$  and the wing angle was  $60\text{--}85^\circ$  at downstroke and  $10\text{--}40^\circ$  at upstroke.

A *Lestes viridis* male showed a nearly horizontal stroke direction when flying backward after an attack on a tandem of *Lestes virens*. The highest flight speed was reached at a downstroke (about  $0.48 \text{ m s}^{-1}$ ). The downstrokes were shorter than the upstrokes (1:1.44,  $N = 2$ ).

Males of *Erythromma viridulum* in territorial disputes very often flew backward. Flying slowly backward was done by phase-shifted stroking at a flight speed of  $0.79 \text{ m s}^{-1}$  at a frequency of 46.2 Hz by a nearly horizontal stroke direction. The downstrokes were shorter than the upstrokes (1:1.5). In three strokes 54.5% of the duration was done phase-shifted and 45.5% in-phase.

## 2.2. Flying fast backward by in-phase stroking

Fast backward flight was done by *Erythromma viridulum* males by in-phase stroking. The flight speed was  $1.16 \text{ m s}^{-1}$  at 55 Hz ( $N = 3$ ). The relation of down- to upstroke was 1:1.27. The speed of the wing tip was calculated to average  $3.8 \text{ m s}^{-1}$  for one upstroke. Calopterygidae normally fly in-phase and at low stroke frequencies from 10 to 20 Hz, depending on whether they make shorter or longer, or no, pauses at the end of upstrokes. In this backward flight one male of *Calopteryx virgo* always made such pauses (43.4% duration of total stroking duration). Ten strokes were done in  $0.82 \text{ s}$  ( $= 12.5 \text{ Hz}$  stroke frequency). He showed nine strokes in backward flight covering a distance of  $0.37 \text{ m}$ , losing height of about 3 cm in the first half of the course. One measured wing tip speed was  $2.35 \text{ m s}^{-1}$ .

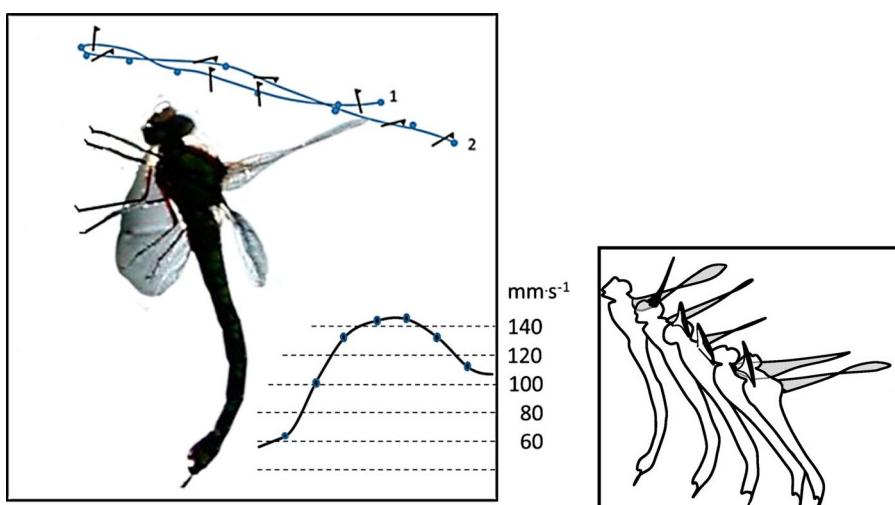


Figure 8. Backward flight of *Aeshna cyanea* female. Left: The track of the tip of the left forewing during one stroke of backward flight (same as Figure 7) beginning at 1 with beginning of downstroke to the end of the successive upstroke at 2. Some wing chords are depicted. The small triangles at the chords mark the leading edge and the upper side of the forewing. The resulting angles of inclination are at downstrokes between  $55^\circ$  (distal) and  $70^\circ$  (basal) in the middle of that phase and in upstrokes between  $5^\circ$  (distal) and  $30\text{--}40^\circ$  (basal). In the right corner below, the flight speed shows a steady acceleration. From dot to dot =  $0.02 \text{ s}$ , total 7 strokes. Right: Successive strokes of the same backward flight in the middle of upstrokes (steep inclined wings) and downstrokes (slightly inclined wings partly distorted). From a film at  $500 \text{ f s}^{-1}$ .

### 2.3. Changing from phase-shifted to in-phase stroking

A courting *Calopteryx splendens* male flew courting in the counter-stroking mode, when for one stroke he flew fast backward in-phase. By this single stroke he covered 0.06 m in about 0.08 s (Figure 10). This is an acceleration of  $9.2 \text{ m s}^{-2}$ .

## 3. Sharp acceleration to escape a frog's attack

A dragonfly fleeing for its life at a frog attack needs the maximum flight capability. Frogs are major hunters of Odonata. They sit hidden and wait until the jumping distance to the prey is promising. When the Odonata recognise the frog, the speed and direction of their fleeing flight is a question of life and death. So all flight actions must be fast and correct.

### 3.1. *Anax imperator* fleeing forward

*Anax imperator* lays eggs endophytically, which means the females have to sit on plants to drill holes for depositing eggs. This is a handicap when frogs attack.

To get out of the water and out of the reach of the frog, the dragonfly first beat its wings in-phase three times at large stroke angles (about  $85^\circ$ ), nearly clapping them together (the last of these three strokes is depicted in Figure 11, being here the first from left). The next three strokes were done at smaller stroke angles (around  $40^\circ$ ) with very short upstrokes and with then high-inclined wings. With the first three strokes at take-off *Anax* reached a distance of 1.2 cm, with the next three strokes 3.7 cm.

These last three upstrokes lasted only  $8 \times 10^{-3}$  s each. They were significantly shorter than the downstrokes ( $= 14 \times 10^{-3}$  s;  $p = 0.014$ , Mann–Whitney,  $N = 6$  wb). The relation between downstroke to upstroke was 1.4: 1 ( $N = 6$ ). The stroke frequency was 40.9 Hz (SD 3.64,  $N = 6$ ).

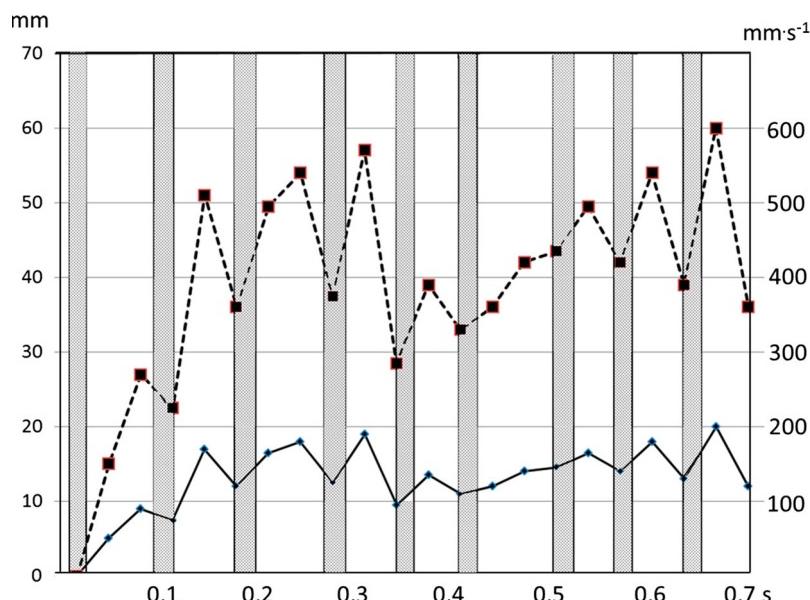


Figure 9. Flight speed (broken line above, right ordinate) and distance gain at each 0.033 s (solid line bottom, left ordinate) in backward flight with nine strokes of a *Calopteryx virgo* male. Grey areas: downstrokes, white areas: upstrokes plus wing standstills. Abscissa: time in seconds. From a film at  $300 \text{ f s}^{-1}$ .

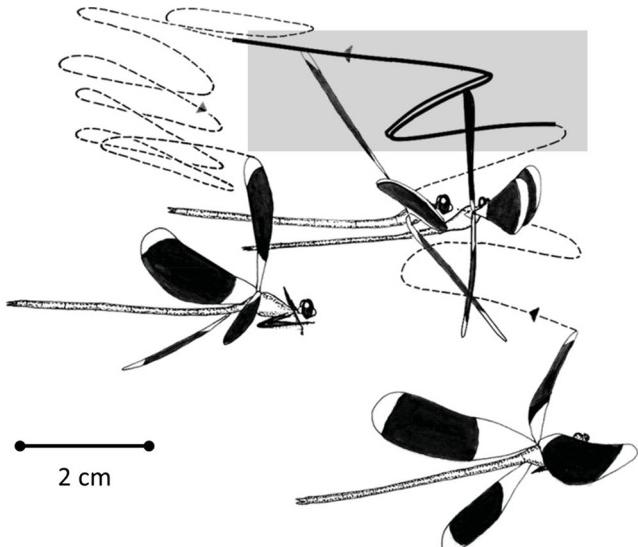


Figure 10. A courting male *Calopteryx splendens* used in-phase stroking (grey areas) to suddenly fly back in between counter-stroking courting flight. The path of the left forewing is depicted during counter-stroking beating (broken line) and in-phase beating (solid line, double solid line = downstroke), small arrows = stroke direction. The figures at top right show the male at upstroke (left figures) and at downstroke (right figure). Drawn by D. Hilmert-Rüppell.

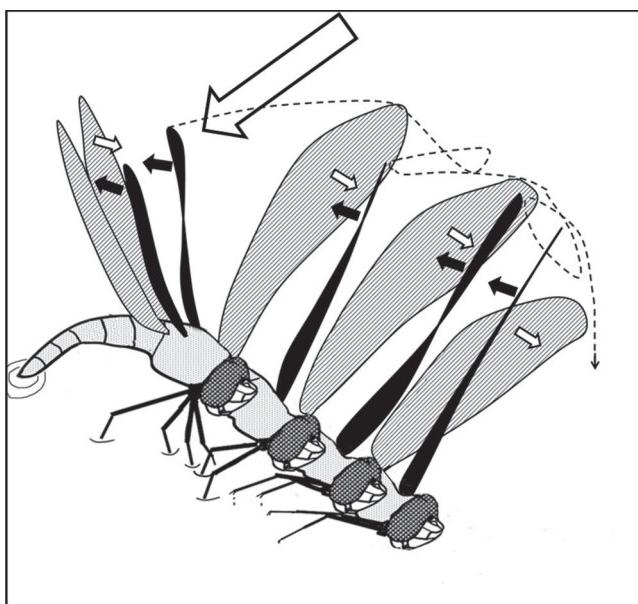


Figure 11. Fast forward flight (beginning from left) of a female *Anax imperator* from egg-laying to escaping an attacking frog (clear arrow: frog's jump). On the first stroke, both wing pairs are depicted at the end of the upstroke to show the large amplitude to nearly flapping together. All strokes were done in-phase. In the next three strokes, only the left wings are shown in the middle of the downstrokes (striped) and in the middle of the upstrokes (black). The arrows show the stroke direction. The dragonfly first lifted its body out of the water and then accelerated forward and downward out of reach of the frog. Broken line: path of the left forewing. The first beats were done in a more horizontal direction, the next three beats increasingly more downward.

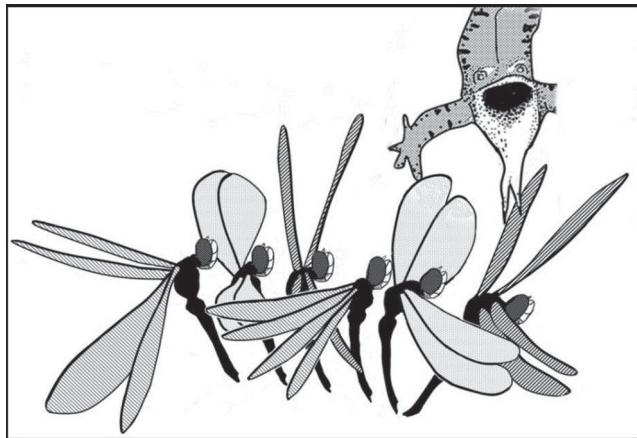


Figure 12. Fleeing flight backward of a female *Leucorrhinia pectoralis* ovipositing from flight. The frog missed this female only by a few millimetres. When the frog started, she changed from phase-shifted stroking to in-phase stroking. Furthermore, the stroke direction was raised to a nearly horizontal stroking and the wing angles were varied: at upstrokes (light grey) they were small and at downstrokes (dark grey) they were large. At the end of the first upstroke (third figure from right) the wings were clapped nearly together. Filmed at  $600 \text{ f s}^{-1}$ .

Figure 11 shows the differences in inclination of the wings at down- and upstroke. Depending on the twisting of the wings, at upstrokes this ranges from about  $40^\circ$  at the base to more than  $80^\circ$  towards the wing tip. At downstrokes, the wings were inclined only a little – about  $5\text{--}10^\circ$  to the stroke direction. At the third downstroke, a speed of the wing tip up to  $6 \text{ m s}^{-1}$  was reached; at upstrokes 2 and 3 of Figure 11 the wing tip reached a speed of  $3.1 \text{ m s}^{-1}$ .

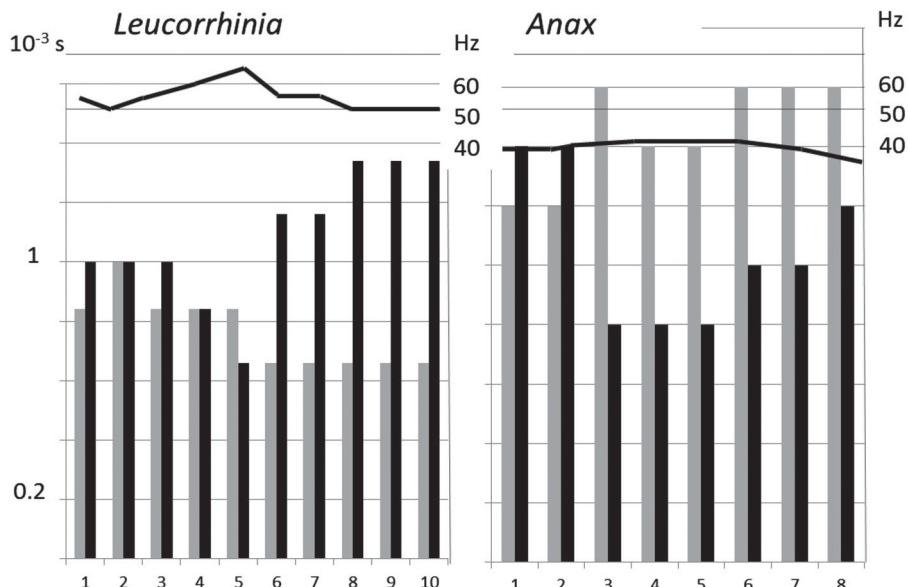


Figure 13. Duration (left ordinate) of successive downstrokes (grey) and upstrokes (black) in *Leucorrhinia pectoralis* (left) and *Anax imperator* females (right) fleeing from a frog's attack during oviposition, all in-phase. *Leucorrhinia* flew backward (short downstrokes, phases 6, 7, 8, 9, 10) while *Anax* flew forward (short upstrokes, phases 3, 4, 5, 6, 7). The beat frequencies varied only a little in *Anax* and more in *Leucorrhinia* (black lines and ordinates right). Same actions as in Figures 11 and 12.

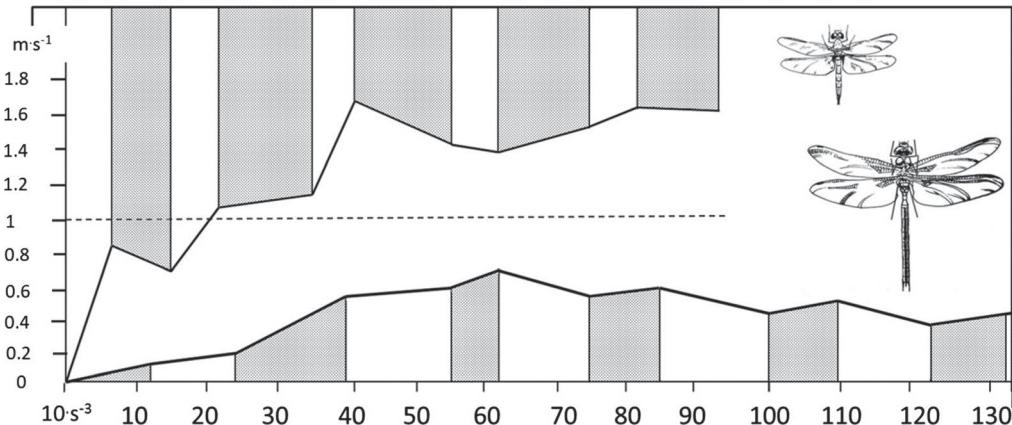


Figure 14. Flight speed of two ovipositing dragonflies fleeing from a frog attack: *Leucorrhinia rubicunda* (above, figures at the same scale) was fleeing backward from hovering and increased speed during downstrokes (white), *Anax imperator* (bottom) which flew forward from sitting, increased speed during upstrokes (grey). The same actions as in Figures 11 and 12. Filmed at  $600\text{ f s}^{-1}$  (Lp) and  $500\text{ f s}^{-1}$  (Ai).

At normal starts after oviposition, the strokes tended to be longer than at fleeing flight (39 Hz,  $N=6$ , SD 2.1;  $p = 0.485$ , Mann–Whitney) and the stroke angles (around 40–50°) were also smaller. The main differences were the shortness of the upstrokes (relation of down- to upstroke was 0.97:1) and the smaller inclination of the wings at upstrokes, which was in a range of 30–45° in the middle of upstroke at normal take-off. This female reached a flight speed of  $370\text{ mm s}^{-1}$  – about half of the speed of the fleeing female.

### 3.2. *Leucorrhinia pectoralis* *fleeing backward*

*Leucorrhinia pectoralis* as a libellulid oviposits in flight. This allows a quick start for fleeing (Figure 12). This small dragonfly reached a velocity of  $0.6\text{ m s}^{-1}$  after only the first downstroke, which lasted  $6.7 \times 10^{-3}\text{ s}$ . The stroke frequency was 53.5 Hz (SD 7.1,  $N=6$ ). The ratio of upstrokes to downstrokes was 1.75:1. The calculated mean wing-tip speed at the short downstrokes was  $8.6\text{ m s}^{-1}$ ; at the longer upstrokes it was about  $5\text{ m s}^{-1}$ . The acceleration was high:  $97.4\text{ m s}^{-2}$  at the first downstroke and  $38.1\text{ m s}^{-2}$  after three downstrokes and two upstrokes.

*Leucorrhinia pectoralis* at normal flight at oviposition had a lower stroke frequency – 44.2 Hz ( $N=12$ ) ( $p > 0.05$  t-test, Mann–Whitney) than at fleeing flight and an equal relation between duration of downstroke to upstroke (0.99:1 down:up). The calculated wing-tip speed in normal oviposition flight was 2.8 to  $3\text{ m s}^{-1}$  for both down- and upstroke. The stroke angles in fleeing flight were large; the wings at the end of upstrokes clapped nearly together.

*A. imperator* flew forward, while *L. pectoralis* flew backward. In both cases the stroke phases directed to the frog were the shortest (Figure 13) and were done by high-inclined wings. These were the phases where the flight speed increased (Figure 14).

### 4. Comparisons of all investigated flights

In forward flight *Calopteryx splendens* males covered by far the longest distance with one wing beat. This was the case in flights pursuing females. The second-highest value was achieved by an *Anax imperator* male. But he was in at a speed of about  $4\text{ m s}^{-1}$  before. Very small values were achieved by an *A. imperator* female fleeing a frog attack, a *C. splendens* male pursuing a

female in courting flight and an *E. viridulum* male in slow forward flight. Non-dimensional flight velocities showed similar relations.

The acceleration was highest in a *Leucorrhinia pectoralis* female fleeing backward, followed by *Anax imperator* in forward flight and an *Erythromma viridulum* male and *Calopteryx virgo* in fast backward flight (Table 2).

## Discussion

This paper confirmed some of the findings of earlier kinematic studies on Odonata flight (Rüppell, 1989). Furthermore, it is encouraging to verify in nature many of the sophisticated results from aerodynamic experiments or calculations (Bomphrey et al., 2016).

It was possible to ascribe an increase of wing inclination angles to different acceleration manoeuvres, as shown by Thomas et al. (2004). We found that increasing stroke angles, stroke frequencies, or both (Figures 3, 4, 6) may also contribute to acceleration.

In rapid acceleration, the shift from phase-shifted to in-phase stroking combined with high-inclined wings at the stroke phases opposite to the flight direction has been confirmed in both forward and backward flight (Figures 5, 6, 9, 10, 11). The phase-shifted flight is the most economical way to fly, but does not produce the most power. This can be realised better by in-phase stroking (Bomphrey et al., 2016; Lehmann, 2017; Thomas et al., 2004; Wang & Russell, 2007). As the volume of the wash grows three-dimensionally while the wing area grows only two-dimensionally, it is clear that two wing pairs in-phase at one time can generate a larger air flow, i.e. a bigger momentum, than only one wing pair after the other in phase-shifted mode. To create a strong flow (heavy wash), these high-inclined stroke phases were very short (Figures 9, 12), when the Odonata were flying for their life during frog attacks.

The flight speed in the fleeing flights increased more in the first three downstrokes of backward flight in the *Leucorrhinia rubicunda* female, than in the upstrokes of the forward-fleeing *Anax imperator* female (Figure 14). This might be due to the fact that Anisoptera possess heavier muscles generating the downstrokes than upstrokes (Büsse & Hörschemeyer, 2013; Pfau, 1986).

In other cases, when low acceleration was required, a phase-shifted backward flight (Figure 8) gave a steadier flight, which is economical, because frequent accelerations are not necessary as they are in unsteady flight. But here again, the inclination angles were larger in downstrokes (opposite to the flight direction) than in upstrokes.

It was impressive to find that even teneral *Coenagrion puella* used the in-phase high-inclined stroke mode to flee fast backward during its first flight. That means that the programmed neuromuscular pattern of this manoeuvre was already functioning in this young individual. We found this pattern in quick backward flight in all investigated species (Rüppell, 1989). Even the large pseudostigmatine *Mecistogaster ornata*, which normally flies using phase-shifted or counterstroking, flew backward for one or two in-phase strokes when getting out of a spider's web where it had tried to forage (Rüppell & Fincke, 1989).

The very effective strokes of *Calopteryx* species are particularly outstanding. These middle-sized damselflies have a very low wing-loading and relatively long wings (Rüppell & Grabow, 1995), generating by far the highest values in forward and backward flight in wing distance per wing beat and non-dimensional flight velocity (Tables 3, 4). At the other end, the acceleration values of the teneral *Coenagrion puella* (Table 2) were low: this damselfly was not yet fully sclerotised.

Odonata show their full flight ability only in nature. They need an open space for their activities, and their sensory system only works properly in undisturbed surroundings. The flights with the highest manoeuvrability, acceleration or speed were found in nature under extreme conditions, mostly at escape flight. In this situation there is often a genuine race between dragonfly and

predator, and to survive, Odonata show incredibly fast manoeuvring by ultrashort wing adjustments. The *Anax imperator* female changed her wing kinematics during the rapid approach of a frog within 0.001 s. The first three strokes after detecting the frog were done at large amplitude, ranging over the space above the dragonfly's body. But as the frog came close very rapidly, the wings were beaten more forward and downward, out of the frog's reach. A *Leucorrhinia pectoralis* individual changed wing kinematics very fast: phase-relationship from shifted to in-phase and down-upstroke relation and inclination within 0.04 s.

Catching prey also requires extreme flight methods, depending on the kind of prey and weather conditions. In some situations, dragonflies seem to be quite successful (Combes, Rundle, Iwasaki, & Crall, 2012; Olberg, Worthington, & Venator, 2000), but with better-flying prey in the field and changeable air currents, the failure rate is much higher (unpublished observation of *C. splendens*). The main impediments causing failures are the fast and erratic flight and the unpredictability of small insect flight courses.

The different amount of flight muscle in relation to body size (Marden, 1989) between dragonflies and damselflies would suggest a different flight behaviour between these two suborders. But the main measures in the investigated manoeuvres were very similar. Dragonflies reached higher flight speeds. Damselflies' stroke directions seem to be wider and more horizontal.

Table 3. Forward flight: distance per wing beat (= dist wb, mm, second row) and non-dimensional flight velocity (= ndfv, third row) of Odonata species (first row) in forward flight. Ev fast = *Erythromma viridulum* male in fast forward flight; Ev slow = *E. viridulum* male in slow forward flight; Cs in-ph = *Calopteryx splendens* male pursuing females (by in-phase stroking); Cs counter = *C. splendens* male pursuing a female in courting flight (counter-strokingly); Ai pursu = *Anax imperator* male pursuing another male; Ai flee = *A. imperator* female fleeing a frog attack. Grey rows = in-phase stroking.

Species	dist wb mm	ndfv
Ev fast	46.4	2.57
Ev slow	31.8	1.77
Cs in-ph	158	5
Cs in-ph	210.8	6.7
Cs counter	27.75	0.88
Ai pursu	149.8	3.11
Ai flee	11.5	0.24

Table 4. Backward flight: Distance per wing beat (= dist wb, mm, second row) and non-dimensional flight velocity (= ndfv, third row of Odonata species (first row) in backward flight. Ev fast = *Erythromma viridulum* male in fast backward flight; Ev slow = *E. viridulum* male in slow backward flight; Cv in-ph = *Calopteryx virgo* male in male–male contest (by in-phase stroking); Cs in-ph = *C. splendens* one in-phase stroke in between courting flight (counter-strokingly); Ac = *Aeshna cyanea* female flying back from a perch; Lp flee = *Leucorrhinia pectoralis* female fleeing a frog attack. Grey rows = in-phase stroking.

Species	dist wb mm	ndfv
Ev fast	32.5	1.8
Ev slow	24.2	1.3
Cv in-ph	41.3	1.31
Cs in-ph	63.3	2
Ac	14.3	0.3
Lp flee	27.4	0.87

The success of Odonata is certainly a result of flight ability. Very different from the flight of all other insects, odonatan flight is diverse and powerful. It enables these insects to fly with relatively large bodies and to be highly successful predators.

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